

A new subspecies of mountain tanager in the *Anisognathus lacrymosus* complex from the Yariguíes Mountains of Colombia

by Thomas M. Donegan & Jorge Enrique Avendaño

Received 7 May 2009

SUMMARY.—A new subspecies of *Anisognathus lacrymosus* is described from Serranía de los Yariguíes in the East Andes of Colombia. The new taxon differs in a combination of plumage characters, including a darker back and crown, from the geographically proximate subspecies *A.l. tamae*, *A.l. pallididorsalis* and *A.l. olivaceiceps* of the East and Central Andes, as well as, on average, having a longer tail than other East Andes populations. The darker plumage of the new subspecies resembles that of *A.l. intensus* of the West Andes (which also occurs in more humid habitats), presenting a 'leap-frog' pattern of geographic variation. The new subspecies is restricted to páramo and stunted Andean ridgetop habitats, apparently being endemic to the Yariguíes massif. Analyses of biometrics, plumage and voice support species rank for *A. (lacrymosus) melanogenys* of the Santa Marta Mountains, as previously suggested by some authors. Subspecies *A.l. melanops*, *A.l. pallididorsalis*, *A.l. yariguierum* and *A.l. lacrymosus* represent phylogenetic species based on plumage, but a greater vocal sample is required to further analyse the rank of these and other populations.

Limits in the Thraupidae (tanagers) have recently been revised (e.g. Burns 1998, Remsen *et al.* 2009) and the family is now considered to be largely restricted to the Neotropics. Many species are brightly coloured and relatively easy to observe, factors which have led to the group being better studied than many other Neotropical bird families (e.g. Isler & Isler 1999).

The mountain tanager genus *Anisognathus* comprises two well-defined groups that have previously been treated in separate genera. 'Core' *Anisognathus* comprises Lachrymose (Lacrimose) Mountain Tanager *A. lacrymosus*, Scarlet-bellied Mountain Tanager *A. igniventris* and Santa Marta (Black-cheeked) Mountain Tanager *A. melanogenys*. In Colombia, these three species generally occur at higher elevations and in lower forest strata than congeners in primary habitats. Blue-winged Mountain Tanager *A. somptuosus* and Black-chinned Mountain Tanager *A. notabilis* are more robust birds with stronger flight and were previously treated as part of the genus *Compsocoma* (e.g. Hellmayr 1936, Zimmer 1944) but were lumped (with little justification) into *Anisognathus* by Meyer de Schauensee (1966). We treat *Compsocoma* as a subgenus of *Anisognathus* herein. *Anisognathus* is restricted to montane South America (Isler & Isler 1999) and has been considered related to various other montane tanager genera such as *Bangsia*, *Buthraupis*, *Chlorornis*, *Dubusia* and *Delothraupis* (Burns & Naoki 2004, Bleiweiss 2008).

Eight subspecies of *A. lacrymosus* are currently recognised, from Venezuela south to Bolivia (Dickinson 2003). These subspecies vary, among other characters, in: the shade of yellow-orange on the underparts; the shade of blue-grey on the crown, back, rump and flight feathers; facial plumage coloration; and the location, size and shape of yellow 'tear' marks on the head. Santa Marta Mountain Tanager *A. melanogenys* has sometimes been treated as conspecific with *A. lacrymosus*, as discussed further under 'Species limits'.

Here, we describe a new subspecies of *A. lacrymosus* recently discovered in the Yariquíes Mountains of Colombia (Donegan *et al.* 2007) and discuss geographical variation in the species in the northern Andes. Species limits and English names herein follow Salaman *et al.* (2009), with alternative names used by Remsen *et al.* (2009) also mentioned.

Methods

Field work.—Between January 2003 and January 2006, we and others studied eight primary forest sites at 150–3,200 m on both slopes of Serranía de los Yariquíes, an isolated western spur of Colombia's East Andes in dpto. Santander. The Yariquíes Mountains are isolated from the rest of the East Andes to the north and east by the dry Sogamoso and Suárez valleys, and to a lesser extent to the south by depressions associated with the ríos Horta, Quirola and Opón, and their tributaries, at least above the 2,500 m contour (Donegan *et al.* 2007).

Study sites were subject to 4–6 days' field work using mist-netting (up to 220 m of mist-nets) and observations including sound-recording and playback. The highest-elevation site studied on the west slope (Lepipuerto, on the upper río Chimera, El Carmen / Simacota municipality, 06°27'29"N, 73°27'27"W; 2,900 m) was accessed by helicopter in January 2005. Here, TMD mist-netted and photographed two individuals of *A. lacrymosus* and made various observations and sound-recordings. At another páramo site on the east slope of the massif studied six months later (Filo Pamplona, Galán municipality; 06°38'18"N, 73°24'32"W; 3,200 m), we mist-netted 11 individuals, made additional observations, and took photographs and blood samples (deposited at Universidad de los Andes). Because distribution maps in the major field guides for the region (Hilty & Brown 1986, Ridgely & Tudor 1989) showed *A. lacrymosus* to be widespread in Colombia's Eastern Andes, no special attention was paid to the species at the time.

On comparing our photographs with other texts (Fjeldså & Krabbe 1990, Isler & Isler 1999) and with specimens, it became apparent that the range of *A. lacrymosus* in the Eastern Andes is less widespread than sometimes stated and that the Yariquíes population showed plumage differences from all other Colombian populations, revealing an undescribed subspecies to be involved (Donegan *et al.* 2007, 2008). JEA collected specimens of the new subspecies at Alto Cantagallos, Finca Santo Domingo, San Vicente de Chucurí municipality, dpto. Santander on the west slope of the Yariquíes massif (06°48'49"N, 73°21'53"W; 2,450 m) on 9–13 November 2006 and at Filo Pamplona (details above) on 20–25 June 2008. In addition, we undertook joint field work at San Pedro de los Milagros, Antioquia, to collate additional data on *A.l. olivaceiceps* in January 2007. JEA also visited the Perijá Mountains to study *A.l. pallidorsalis* in July 2008 and TMD visited the Santa Marta Mountains to study *A. melanogenys* in January 2009 (see Appendix 1 for locality details).

Museum studies.—We or colleagues working with Project Biomap or at the Phelps collection (Caracas) examined museum specimens or photographs of specimens of *A. lacrymosus* and *A. melanogenys* in the institutions detailed in Appendix 1. We personally inspected or obtained photographs of all known East Andes and 'Bogotá' or 'Colombia' specimens. Soft-part colours and plumage descriptions were taken using codes in Munsell Color (1977, 2000) with blue and yellow hues from Smithe (1975). The following measurements were taken: wing-chord, tail length (to nearest 1 mm), tarsus length, culmen from skull to tip of upper mandible (to nearest 0.5 mm) and mass (g). Data from unsexed or juvenile birds, or those moulting measured feathers were excluded. Biometric data are presented in Appendix 2.

Plumage diagnosis and statistical tests for biometrics.—Subspecies limits were assessed following Donegan & Avendaño (2008) and Donegan (2008), using the following statistical approaches:

LEVEL 1: for biometrics, statistically significant differences at $p < 0.05$ using an unequal variance (Welch's) t -test. A Bonferroni correction was applied for biometric data (five variables), to produce $p < 0.01$. This test was not applied to assess plumage differences. The Level 1 calculation assesses statistical significance, but tolerates considerable overlap. Further calculations, described below, were undertaken to measure inter-population differences in the context of various species and subspecies concepts. In the formulae used below, \bar{x}_1 and s_1 are the sample mean and sample standard deviation of Population 1; \bar{x}_2 and s_2 refer to the same parameters in Population 2; and the t value uses one-sided confidence intervals at the percentage specified for the lower degree of freedom of the two populations for the relevant variable, with t_1 referring to Population 1 and t_2 referring to Population 2.

LEVEL 2: a '50% / 97.5%' test, following Hubbs & Perlmutter's (1942) now little-used subspecies concept, which is passed if sample means are two standard deviations or more apart, here defined as the sample mean of Population 1 falling outside the range of 97.5% of Population 2, controlling for sample size:

$|(\bar{x}_1 - \bar{x}_2)| > (s_1(t_{1@97.5\%}) + s_2(t_{2@97.5\%}))/2$. This test was not applied to assess plumage differences.

LEVEL 3: the traditional '75% / 99%' test for subspecies (Amadon 1949, Patten & Unitt 2002), modified to control for sample size:

$$|(\bar{x}_1 - \bar{x}_2)| > s_1(t_{1@99\%}) + s_2(t_{2@75\%}) \text{ and } |(\bar{x}_2 - \bar{x}_1)| > s_2(t_{2@99\%}) + s_1(t_{1@75\%})$$

For plumage differences, this test was deemed satisfied for populations which are distinctive in plumage but which showed intergradation with geographically proximate populations.

LEVEL 4: for biometrics, diagnosability based on recorded values (first part of Isler *et al.*'s 1998 test and essentially equivalent to Cracraft's (1983) phylogenetic species concept). For phenotypic differences, Level 4 diagnosability was deemed to be satisfied for assumed allopatric populations that showed diagnosable differences based on available samples.

LEVEL 5: for biometrics, so-called '95% / 95%' diagnosability (i.e. 97.5% / 97.5%, given that the lower 2.5% of each population is also outside the range of each population). This occurs when sample means are four standard deviations apart, controlling for sample size, and is the second part of Isler *et al.*'s (1998) diagnosability test and also essentially equivalent to Cracraft's (1983) phylogenetic species concept:

$$|(\bar{x}_1 - \bar{x}_2)| > s_1(t_{1@97.5\%}) + s_2(t_{2@97.5\%})$$

For determining subspecies rank, Isler *et al.* (2006, 2007) suggested a 'full diagnosability for one character' test to diagnose subspecies of Thamnophilidae (Level 4 / 5 for at least one variable: essentially a phylogenetic species with small differences). The traditional test in ornithology for diagnosing subspecies is the Level 3 '99% / 75%' test. Stiles & Caycedo (2002) ranked allopatric populations with statistically significant means for different variables (Level 1) subspecifically. Where allopatric populations meet Levels 1, 3 and 4 / 5 for at least one character (i.e. satisfy all subspecies definitions), we proposed the description of new subspecies. Synonymy of subspecies was proposed only if allopatric populations failed to achieve any level of diagnosability (i.e. do not pass any subspecific definitions). Other putative subspecies are discussed but not described. This approach might produce inconsistency, because historically recognised but dubious taxa maintain their status, but similarly differentiated undescribed populations continue to lack nomenclatural status. However, this approach results in high thresholds for both new taxa and synonymy and permits maintenance of current taxonomic treatments for other populations pending molecular or other studies.

Vocalisations.—Sound-recordings were made using a Sony MiniDisc and Vivanco EM35 microphone, and have been deposited at the British Library (London), Banco de Sonidos Animales of Instituto Alexander von Humboldt (Villa de Leyva, Colombia), and at www.xeno-canto.org (XC). Due to the small number of recordings available for many populations, especially *A.l. tamae*, only subjective comparisons with vocalisations of other *Anisognathus* taxa were made.

Distribution modelling.—Data on localities for *A. lacrymosus* in Colombia were obtained from DATAVES, Fundación ProAves, Instituto Alexander von Humboldt and other sources (see Appendix 1). Locality data were geo-referenced for Colombian and Venezuelan localities using specimen data, publications in which records are found, data from observers, Paynter (1982, 1997) and other sources. All specimen, sound-recording, photographic and sight record localities were plotted, and models of potential distribution were constructed by J. Velásquez using MAXENT 3.0 (Phillips *et al.* 2006) based on climate data obtained from Worldclim (Hijmans *et al.* 2005). For most specimen localities, data were only available to the nearest minute. Minute accuracy was therefore used as a standard for geo-referencing all localities. This is considered a reasonable approach to ensure consistency within the dataset and in light of other constraints of such modelling, including the lack of actual (as opposed to modelled) climatic data for much of the northern Andes and the Yariguíes range in particular. Each species and subspecies was analysed separately, with the exception of *A.l. olivaceiceps*, *A.l. palpebrosus* and *A.l. caerulecens*, which are continuously distributed and were therefore analysed together. This approach resulted in analyses of the potential distributions of certain subspecies being based upon few localities. However, the modelling approach used herein is considered good for taxa with 20 or more localities and reasonable for taxa with *c.*5–20 localities (following Pearson *et al.* 2007). For taxa with fewer localities, the analysis is presented subject to caveats. The predicted ranges of each subspecies were then converted to presence-absence maps using a 20th percentile training presence threshold, which is the probability at which 20% of the training presence records are omitted. This threshold, although arbitrary, was chosen to avoid bias by outlying records or records geo-referenced inaccurately. Finally, predicted ranges for any subspecies or subspecies-group falling outside of regions continuous with known localities were excluded. The model was not refined to consider potentially suitable (e.g. non-modified) habitats.

Description

The population of *Anisognathus lacrymosus* occurring in Serranía de los Yariguíes is diagnosably distinct in plumage from all other subspecies. A new taxon that is a phylogenetic species (Cracraft 1983) or subspecies (Isler *et al.* 1998), in the sense of the tests set out above is clearly involved. We propose that it be named:

Anisognathus lacrymosus yariguierum subsp. nov. Yariguíes Mountain Tanager

Holotype.—Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia (ICN 36902). Adult male collected by Jorge Enrique Avendaño on 22 June 2008 (original number JEA-650) in *páramo* at Filo Pamplona above Finca La Aurora, municipality of Galán, dpto. Santander, Colombia (coordinates above) on the east slope of the Yariguíes massif, just below the main ridgeline. Skeleton with muscle and other soft tissue preserved in 70% ethanol deposited at Laboratorio de Biología Evolutiva de Vertebrados, Universidad de los Andes. Tissue samples have been deposited at the Banco de Tejidos of Universidad de los Andes (UniAndes-BT 700) and Banco de Tejidos of Instituto Alexander von Humboldt, Palmira, Colombia (IAVH-BT). The holotype is shown in Figs. 1(i), 2(iv) and 3(i).

Allotype and paratypes.—The type series is shown in Fig. 3. All were collected by Jorge Enrique Avendaño. The first is designated as an allotype, the others as paratypes. ICN 36903 / UniAndes-BT 701: (allotype) adult female captured at the type locality with the holotype and probably its mate (skull 100% ossified, follicular ovary 7.7×3.5 mm with largest follicle 0.5 mm, some subcutaneous fat in neck, furculum and flanks, 37 g, wing, tail and body moult); previously captured on 13 July 2005 at 13.30 h, and banded with ProAves ring no. C02784 (still on the specimen's leg). ICN 36911 / UniAndes-BT 702: immature male collected at the type locality on 23 June 2008 (skull ossification <50%, both testes yellowish, left testis 2.4×1.5 , right testis 2.0×1.3 , abundant subcutaneous fat in throat, neck, furculum, breast and dorsal regions, 38 g, wing and tail moult). ICN 36918 / UniAndes-BT 703: immature male collected at the type locality on 25 June 2008 (skull 30% ossified, left testis yellowish 1.7×1.5 , right testis blackish 2.0×1.5 , some subcutaneous fat in neck, furculum, flanks and back, 37 g, wing, tail and body moult). ICN 36920 / UniAndes-BT 704: juvenile female collected at the type locality on 26 June 2008 (skull 0% ossified, smooth ovary 3.0×2.7 , abundant subcutaneous fat in throat, furculum and flanks, 32 g, negligible body moult). ICN 36176 / UniAndes-BT 546: adult female collected at Alto Cantagallos, San Vicente de Chucurí municipality on the west slope of Serranía de los Yariguíes (coordinates above) on 13 November 2006 (skull 50% ossified, follicular ovary 6.2×3.2 with largest follicle 1.7 mm, some subcutaneous fat in neck and furculum, 35 g, wing and body moult). Tissue samples of the allotype and paratypes have also been deposited at IAVH-BT.

Diagnosis.—*A.l. yariguierum* is clearly a member of the genus *Anisognathus* and the *A. lacrymosus* species-group on the basis of its plumage (e.g. Fig. 2), vocalisations (e.g. Figs. 5–6) and biometrics. It differs from *A.l. tamae* of the East Andes, *A.l. pallididorsalis* of the Perijá Mountains and *A.l. olivaceiceps* of the northern Central Andes in its darker and bluer crown, darker mantle, darker blue rump and shoulder, and darker face with less strong yellowish tones. It differs further from *A.l. tamae* and *A.l. pallididorsalis* in its darker tail and less extensive blue markings on the rectrices. The new subspecies differs from *A.l. melanops* of the Venezuelan Andes in having darker upperparts. The head and mantle of the new subspecies are closer to *A.l. intensus*, which occurs in the southern West Andes of Colombia. However, *A.l. yariguierum* differs from the latter subspecies in its more bluish crown, face, nape and mantle. Compared to *A.l. palpebrosus* of Ecuador and southernmost Colombia, and the southern races *A.l. caeruleus* and *A.l. lacrymosus*, it has a bluer crown, darker back, darker blue rump, darker yellow underparts, and darker blue primary remiges. It can be separated from *A. melanogenys* by the presence of a yellow 'tear' on the nape, the darker blue crown and blue (not greenish) back, tail and wing, and shorter bill. It lacks the red underparts of Scarlet-bellied Mountain Tanager *A. igniventris* and has less extensive black feathering on the upper breast. Members of the subgenus *Compsocoma* do not closely resemble *A.l. yariguierum*.

Description of the holotype.—Crown dark bluish (73, Indigo). Sides of head and moustachial region dark, with faint yellowish tinge (5YR 2.5/2). Elongated, tear-shaped spots below eye and below and behind ear-coverts dark yellow (18, Orange Yellow). Mantle dark grey with hint of blue (Gley 2, 3/5 PB but bluish). Rump and shoulder feathers tipped blue (between 70, Smalt Blue and 71, Campanula) with unexposed dusky bases resulting in overall blue coloration over this region. Tail dusky (10YR 2/1) with outer remiges faintly tipped blue (as flight feathers). Outer remiges of alula and all wing-coverts tipped blue (as rump) otherwise dusky (10YR 2/1). Primaries, secondaries and tertials dusky (10YR 2/1) with outer remiges, except the outermost primary, tipped light blue (66, Sky Blue, slightly darker on tertials). Underparts orange-yellow (closest to 18, Orange Yellow, but darker), feathers being dusky (10YR 2/1) at base, with darker feathering exposed only slightly on



flanks and tibia. Irides dark brown, bill black, tarsi, feet and nails black-brown, soles dark ochre. Flattened wing (after collection) 92.2 mm, tail 77.3 mm, tarsus 26.0 mm, culmen to skull 16.4 mm, bill depth (at nostrils) 6.2 mm, bill width (rictus) 11.6, mass 35 g. Fairly extensive subcutaneous fat in dorsal, furculum and neck regions. Body moult restricted to a few feathers in crown, nape, throat, breast, belly and uppertail-coverts, wing moult broadly symmetrical with emergent ninth and eighth primaries on both wings, second to fourth and sixth secondaries on left wing and third, fourth and seventh secondaries on right wing. Tail moult also broadly symmetrical with emergent second and fourth rectrices from outermost on the left side and third and fourth rectrices on the right side. Stomach contents included digested plant material and seeds. Skull 100% ossified. Left testis: 5.0 × 2.5 mm; right testis 4.4 × 2.2 mm.

Variation.—All specimens are essentially identical to the holotype with the following exceptions. Compared to the other specimens, ICN 36920 (a juvenile female) is dorsally duller and more yellowish ventrally. ICN 36176 has more orange underparts compared to the rest (midway between 17, Spectrum Orange and 18, Orange Yellow), resembling *A.l. intensus* even more closely (Fig. 3). Differences between this specimen and the rest of the type series are more notable in photographs than when compared visually. The variation in underparts coloration could represent either individual or geographical variation within *A.l. yariguierum*. The darker breasted specimen was taken 23 km north of the type locality. Birds photographed and released from the southernmost site (Lepipuerto), which like the darker bird were collected on a west-facing slope, are similar in plumage (including underparts coloration) to Filo Pamplona specimens. A juvenile mist-netted and released at Filo Pamplona had a yellowish gape. See Appendix 2 for variation in biometrics.

Distribution.—Fig. 4 shows the localities at which *A.l. yariguierum* has been recorded and the range of *A. lacrymosus* in the northern Andes. *A.l. yariguierum* has been found to date only in Serranía de los Yariguíes, where it is confined to the highest-elevation páramos and subpáramos. Páramo habitats of the Yariguíes Mountains have no connectivity with such habitats elsewhere in the East Andes (Fig. 4). Other recently described taxa including *Scytalopus griseicollis gilesi* (Donegan & Avendaño 2008), *Grallaricula nana hallsi* (Donegan 2008) and the butterfly *Idioneurula donegani* (Huertas & Arias 2007) are also apparently endemic to such

Legends to figures on opposite page

Figure 1 (top). From left to right and top to bottom (i) Holotype of *Anisognathus lacrymosus yariguierum* (J. E. Avendaño); (ii) *A.l. tamae*, Alto Pesebre, Tamá National Park, Herrán, Norte de Santander, East Andes, Colombia (A. M. Cuervo); (iii) *A.l. pallididorsalis*, vereda Sabana Rubia, Manaure, Cesar, Perijá, Colombia (J. E. Avendaño); (iv) *A.l. melanops*, Dinira National Park, Lara, Mérida, Venezuela (J. E. Miranda T.); (v) *A.l. olivaceiceps*, vereda La Lana, San Pedro de los Milagros, Antioquia, Central Andes, Colombia (T. M. Donegan / B. Huertas / J. E. Avendaño); (vi) *A.l. olivaceiceps*, West Andes population, Reserva Natural de Aves Colibrí del Sol, Urrao, Antioquia (A. Quevedo / ProAves); (vii) *A.l. palpebrosus*, Reservas de Aves Comunitarias, Roncesvalles, Tolima (A. Quevedo/ProAves); (viii) *A.l. intensus*, Munchique National Park, El Tambo, Cauca, West Andes, Colombia (Juan Pablo López); (ix) *A. melanogenys*, Reserva Natural de Aves El Dorado, Santa Marta, Magdalena, Colombia (C. Olicaregui / ProAves)

Figure 2 (lower left). Colombian subspecies of *A. lacrymosus*, from left to right: (i) *A.l. palpebrosus* ICN 2816 (La Cocha, Nariño, southern Colombian Andes, collected 2 February 1950 by J. I. Borrero); (ii) *A.l. intensus* ICN 25790 (Farallones de Cali (Alto Pato), Valle del Cauca, Western Andes, collected 29 July 1980 by H. Romero-Z et al.), (iii) *A.l. olivaceiceps* ICN 35001 (Alto Ventanas, Jardín, Antioquia, Central Andes, collected 25 February 2004 by G. Suárez), (iv) *A.l. yariguierum* ICN 36902 (holotype), (v) *A.l. tamae* ICN 18191 (Páramo de Tamá, Toledo, Norte de Santander, Eastern Andes, collected 15 August 1968 by P. Bernal) and (vi) *A.l. pallididorsalis* ICN 36781 (vereda El Cinco, Manaure, Cesar, Perijá, collected 12 July 2008 by J. E. Avendaño) (J. E. Avendaño)

Figure 3 (lower right). Ventral and dorsal views of the *A.l. yariguierum* type series. From left to right: (i) ICN 36902 (holotype), (ii) ICN 36918 (paratype); (iii) ICN 36903 (allotype); (iv) ICN 36911 (paratype); (v) ICN 36920 (paratype); (vi) ICN 36176 (paratype) (T. M. Donegan)

habitats in Yariquíes, and possess essentially identical distributions to *A.l. yariguierum* (see maps in references cited above).

Our own rainfall readings taken in the field and data in Worldclim (Hijmans *et al.* 2005) reveal higher levels of precipitation for sites where *A.l. yariguierum* is predicted to be present in Serranía de los Yariquíes than the average for sites of similar elevation in the East Andes (mean 1,400 vs. 1,900 mm / p.a.: Donegan & Avendaño 2008).

Geographically proximate *A.l. tamae* is found elsewhere in the East Andes but is rare in collections, with few recent observations and is little known in life. Its absence from many localities in the East Andes and the small number of specimens and recent observations are surprising given that *A.l. olivaceiceps* / *palpebrosus* of the Central Andes is so widespread and common.

Elsewhere in Colombia, *A. lacrymosus* is also found in páramos, in shrubby, young regrowth in montane forest and at forest borders at lower elevations. *A. somptuosus* occurs in Serranía de los Yariquíes and elsewhere throughout the Colombian Andes at lower elevations in montane and premontane forest. In the Central Andes, *A. somptuosus* and *A. lacrymosus* are sympatric in secondary forest, but appear to segregate according to habitat use, with the former found more frequently in higher forest strata and the latter generally in lower forest strata or in stunted vegetation. Both species occur at forest borders.

Vocalisations.—Several sound-recordings were made at Lepipuerto (e.g. Figs. 5A, 5B, 5F, 6A, 6B). These have been deposited at the British Library, London, and Instituto Alexander von Humboldt in Colombia and at www.xeno-canto.org nos. XC37291–37303 and XC37310. *A. lacrymosus* taxa possess a varied repertoire of calls and songs. Unlike suboscines (e.g. Kroodsma 1984), oscine vocalisations are not innate and may have a learned component (i.e. they might be affected by environmental factors). As a result,

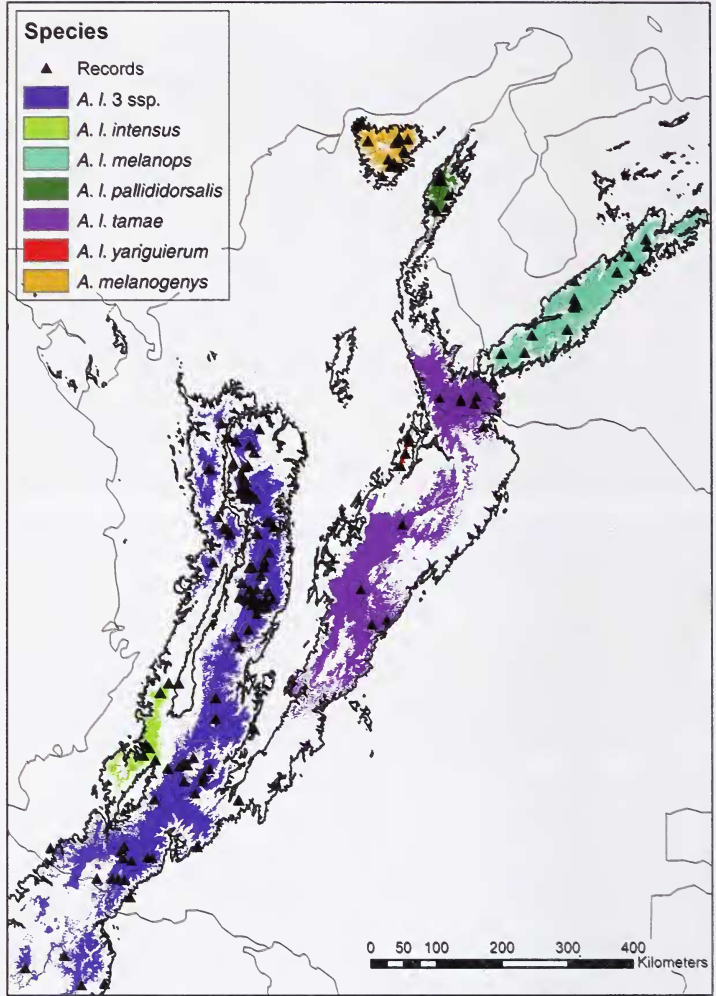


Figure 4. Potential distribution map showing records and modelled potential distribution of *A. lacrymosus* subspecies and *A. melanogenys* in the Colombian Andes.

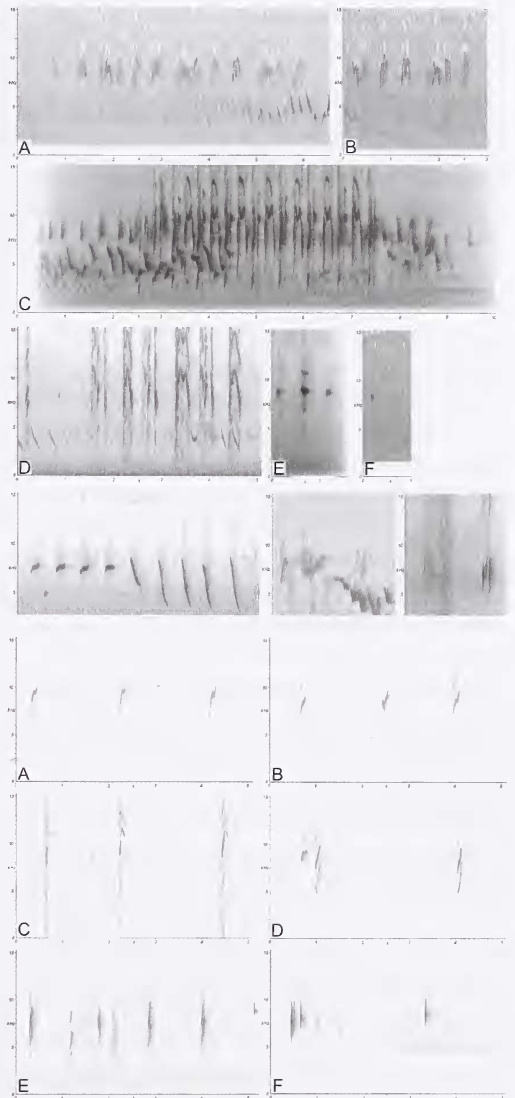
Figure 5 (top). Sonograms of songs of (A) *A.l. yariguierum*, Lepipuerto, Serranía de los Yariguíes (T. M. Donegan: XC 37295), with calls below c.7.5 kHz of Golden-fronted Whitestart *Myioborus ornatus*; (B) As previous (XC 37291); (C) *A.l. palpebrosus*, Neira, La Cristalina, upper río Tapiás, Caldas (A. M. López in Álvarez *et al.* 2007), with calls below 8 kHz of *Myioborus ornatus*; (D) *A.l. caerulescens*, Tapichalaca, Zamora-Chinchipec, Ecuador (N. Krabbe in Krabbe & Nilsson 2003), with calls below 6 kHz probably of Yellow-breasted Brush Finch *Atlapetes latinuchus*. Sonograms of: (E) *A.l. olivaceiceps* contact call, Antioquia, Colombia (Alvarez *et al.* 2007); (F) *A.l. yariguierum* contact call, Lepipuerto, Serranía de los Yariguíes (T. M. Donegan XC 37310); (G) *A.l. caerulescens* dawn song, Cajanuma, Loja, Ecuador (P. Coopmans in Krabbe *et al.* 2001); (H) *A.l. palpebrosus*, Pasto, Nariño, Colombia (O. Laverde: XC 17800); (I) *A. melanogenys* flight call, then call, Reserva Natural de Aves El Dorado, Magdalena, Colombia (T. M. Donegan: XC 37290).

Figure 6 (bottom). Sonograms of calls of (A) *A.l. yariguierum*, Lepipuerto, Serranía de los Yariguíes, Santander, Colombia (T. M. Donegan: XC 37298); (B) As previous (XC 37299); (C) *A.l. melanops*, Guaracamal National Park, Trujillo, Mérida, Venezuela (Boesman 1999); (D) *A.l. pallididorsalis*, El Cinco, Manaure, Cesar, Colombia (J. E. Avendaño); (E) *A.l. palpebrosus*, río Blanco, Manizales, Caldas (M. Álvarez in Álvarez *et al.* 2007); (F) *A. melanogenys*, Reserva Natural de Aves El Dorado, Magdalena, Colombia (Krabbe 2008a).

voice has been little-used to assess species limits in oscines, and tanagers in particular, although there are some recent studies (see e.g. Cadena *et al.* 2007) and vocalisations must possess some innate component as otherwise species would not have different voices. *Anisognathus lacrymosus*, like many oscines, has a variable repertoire (Figs. 4–5).

The song of *A.l. yariguierum* consists of a 2–8 seconds-long, rapidly delivered series of sharp, high-pitched notes, upstrokes and up-down strokes, at c.7.5–10.5 kHz (Figs. 5A–5B). Similar songs are given by *A.l. olivaceiceps*, *A.l. palpebrosus* and possibly some other subspecies (Fig. 5). *A.l. yariguierum* appears to show more deep downstrokes within phrases than that shown on recordings of some other taxa. It is unknown whether differences in note shape reflect individual or geographical variation.

The calls of *A.l. yariguierum* (Figs. 6A–6B) comprise a series of repeated high-pitched, short whistles *suip* with long gaps between them. Each whistle appears on the sonogram as a short, rising, broken, upstroke at c.5–11 kHz and is c.0.1–0.2 seconds-long. Calls are repeated at irregular intervals and vary in note shape. Similar calls of *A.l. palpebrosus* (Fig. 6E) appear less broken in note shape, whilst available recordings of this call in *A.l. melanops* (Fig. 6C) and *A.l. pallididorsalis* (Fig. 6D) show variations in note shape (e.g. *suip-iu* in *A.l. melanops*).



We also recorded a contact call of *A.l. yariguierum* (Fig. 5F), consisting of a soft single note of at c.8–9 kHz, similar to a recorded call of *A.l. olivaceiceps* (Fig. 5E).

Intriguingly, songs of several subspecies of *A. lacrymosus* (including *A.l. yariguierum*) are delivered simultaneously with the song of nearby individuals of Golden-fronted Whitestart *Myioborus ornatus*, *Atlapetes* brush finches and other species that use lower acoustic frequencies (Figs. 5A, 5C, 5D).

Biometrics.—*A.l. yariguierum* is not diagnosable beyond Level 2 in biometrics from any *A. lacrymosus* taxa, with overlap noted for all variables (Appendix 2). However, based on specimen data, the new subspecies has, on average, a longer tail compared to *A.l. melanops* (Levels 1 and 2), *A.l. tamae* (Level 1), *A.l. caerulescens* (Levels 1 and 2) and *A.l. lacrymosus* (Levels 1 and 2). Based on data from live birds, it further appears to have an on average shorter tail than *A.l. olivaceiceps* (Level 1) and *A.l. palpeborus* (Levels 1 and 2). The other Colombian populations (*A.l. pallididorsalis* and *A.l. intensus*) also showed small differences in tail length from *A.l. yariguierum*, but did not meet the requirements of our Level 1 test based on specimen data ($0.01 < p < 0.05$ in each instance) and no data from live birds were available. *A.l. yariguierum* may also have, on average, a longer tarsus than *A.l. pallididorsalis* (specimen data: Levels 1 and 2) and *A.l. palepbrosus* (data from live birds: Level 1) and a longer culmen compared to *A.l. tamae* (specimen data: Level 2), *A.l. pallididorsalis* (specimen data: Levels 1 and 2), *A.l. olivaceiceps* (data from live birds: Level 1) and *A.l. palpebrosus* (data from live birds: Level 1), although observed differences in these two measurements are very small.

Ecology.—*A.l. yariguierum* has been recorded only in pristine primary páramo and ridgetop habitats 2–30 km from settlements. Such sites are subject to very high levels of precipitation, with torrential rain lasting several hours each day of field work and frequent ground-level cloud cover. The new taxon is absent from taller montane or other forest at lower elevations. Birds are often quite visible. In July 2008 and June 2005, small flocks were observed and individuals with gape lines mist-netted. In contrast, only pairs were seen in January 2005. Such behaviour is consistent with nesting in March–April, as is apparently the case for various other species in the Yariguíes region. Ossification and gape line data indicate that adult plumage is attained very rapidly. No specimens of any *A. lacrymosus* races with distinct juvenile or immature plumages were found in collections. We observed *A.l. yariguierum* following mixed-species flocks of Streaked Tuftedcheek *Pseudocolaptes boissonneautii*, Golden-fronted Whitestart *Myioborus ornatus*, Golden-crowned Tanager *Iridosornis rufivertex* and Common Bush Tanager *Chlorospingus ophthalmicus*. *A. lacrymosus* was also observed joining flocks at forest borders in San Pedro de los Milagros (Antioquia: *olivaceiceps*), Manaure (Cesar: *pallididorsalis*) and Suratá (Santander: *tamae*).

Conservation.—*A.l. yariguierum* is endemic to the Colombian East Andes EBA (038: Stattersfield *et al.* 1998). It qualifies for IUCN Category D2 Vulnerable status due to its Area of Occupancy being less than 100 km² and being known from fewer than five localities. The new subspecies is rather common in páramo and ridgetop habitat. Following our work and with the impetus of the Ministerio de Medio Ambiente, Corporación Autónoma Regional de Santander (CAS), various mayoralties of the region and NGOs, the Serranía de los Yariguíes National Park was declared in May 2005. The protected area covers all páramo habitats of the range and should assist in conserving *A.l. yariguierum* and other threatened species (see Donegan & Huertas 2005, Huertas & Donegan 2006). This description does not affect the current IUCN status of *A. lacrymosus* as Low Risk.

Etymology.—The subspecific name, *yariguierum*, to be treated as a noun declined in the genitive plural, which need not agree in gender with the generic name in combination under Art. 31.2.2 of the International Code of Zoological Nomenclature (ICZN 1999). The

name honours the extinct Yariguíes indigenous people and the massif that bears their name, to which *A.l. yariguierum* is apparently restricted. Further details are given in Donegan & Huertas (2006).

Use of genus name *Anisognathus*.—Three genus names for birds in what is currently known as *Anisognathus* were described between the years 1850 and 1852: *Anisognathus* Reichenbach, 1850 / 52; *Compsocoma* Cabanis, 1850 / 51 and *Poecilothraupis* Cabanis, 1850 / 51. The date of publication of these names and priority appears not have been subject to detailed study. Use of the generic name *Anisognathus* herein follows prevailing treatments in modern Neotropical ornithological publications.

Geographic variation in *Anisognathus lacrymosus*.—*A. lacrymosus* includes a number of morphologically different populations found throughout the tropical Andes. It has relatively poor flight for a tanager, making the group excellently suited to studies of speciation and biogeography. However, few authors since Zimmer (1944) have studied geographical variation in the species. Graves (1985) categorised *A. lacrymosus* as exhibiting 'smooth clinal' variation, which is an over-simplification and appears true only of some populations. In contrast, Krabbe *et al.* (2006) discussed the intriguing presence of two rather different subspecies (*A.l. olivaceiceps* and *A.l. intensus*) in the West Andes of Colombia: 'There is indirect evidence that colonisation of the Western Andes in some cases happened by jump dispersal across the Cauca Valley rather than through continuous suitable habitat. One form of Lacrimose Mountain-Tanager (*Anisognathus lacrymosus olivaceiceps*) occurs in the north ends of both cordilleras, whereas the form *palpebrosus* is found further south in the Central Andes and the form *intensus* further south in the Western Andes (to which it is endemic).' Field work within the apparent distribution 'gap' between Risaralda and Valle in the West Andes is needed to consider further the nature of geographic variation in the West Andes.

Graves (1985), Zimmer (1944) and Ridgely & Greenfield (2001) all describe clinal variation in *A. lacrymosus* from northern Peru through Ecuador to the Central Andes of Colombia. Three subspecies occur in this region, from north to south: *olivaceiceps* (type locality: Santa Elena, Antioquia, Colombia), *palpebrosus* (type locality: Pasto, Nariño, Colombia) and *caerulescens* (type locality: Cutervo, Cajamarca, Peru). Our museum work leads us to conclude that *A.l. olivaceiceps* could be recognised under subspecies concepts that permit intergradation or admit taxa that are not wholly diagnosable (e.g. Amadon 1949, Patten & Unitt 2002). Specimens from both the West Andes and Central Andes of Antioquia are consistent in plumage, having a greyer face and paler mantle than specimens from further south. There is a region of intergradation between this subspecies and birds treated as *A.l. palpebrosus* in Tolima (e.g. Fig. 1v), which themselves differ in plumage saturation from Nariño specimens. The proposition that *A.l. caerulescens* represents a valid subspecies with respect to *A.l. palpebrosus* under subspecies concepts based on any of our Levels 2 to 5, is not supported. However, our Level 1 test was passed as between populations north and south of the southern Tungurahua border in Ecuador (c.01°30'S) for tail length based on specimens, and a region of less suitable habitat was predicted in this region by distribution modelling, so we do not formally propose synonymy. There are plumage differences between individuals from the two type localities, but Zimmer (1944) described in detail a gradual shift in a number of these plumage features between these localities, describing it as 'perfect intergradation'. Only one of these three subspecies (*palpebrosus* being senior) would be recognised under subspecies concepts based on full diagnosability (e.g. Zink 2003).

In contrast, the northern races *A.l. pallidorsalis* (Perijá), *A.l. melanops* (Mérida) and *A.l. yariguierum* (Yariguíes), as well as the southernmost *A.l. lacrymosus* (Peru, south of the Marañón Valley) have allopatric distributions with respect to other *A. lacrymosus* taxa and

are diagnosable in plumage from other populations. They all represent phylogenetic species (Cracraft 1983) and meet all subspecies definitions considered here. The sole *A.l. melanops* recording available has a higher frequency than equivalent calls in other subspecies (Fig. 6C) and shows small differences in note shape from other recordings of northern races (Figs. 5–6). *A.l. pallididorsalis* further shows differences up to Level 2 in bill length from all other races except *A.l. tamae* and *A. l. lacrymosus*. Some of these populations or groups thereof might be considered candidates for species rank under some species concepts. However, a thorough vocal study (and greater vocal sample) is needed to consider species limits further. The taxon to which East Andes populations have been assigned, *A.l. tamae*, is unknown vocally but darker individuals within this subspecies are virtually indistinguishable from paler individuals of *A.l. olivaceiceps*. The generally greater differentiation in plumage (and, apparently, voice) in the north of the species' range and presence of *A. melanogenys* in the Santa Marta Mountains is notable and may inform hypotheses concerning the group's radiation.

The darker plumage shared by *A.l. yariguierum* of the East Andes (Yariguíes) and *A.l. intensus* of the West Andes, compared to the paler plumage shared by *A.l. tamae* of the East Andes and *A.l. olivaceiceps* of the Central Andes are intriguing examples of a 'leap-frog' pattern in geographic variation (Remsen 1984). As the Yariguíes Mountains and West Andes share higher levels of precipitation than nearby regions where paler subspecies are found, darker plumage might be a convergent adaptation, conforming to Gloger's Rule (Zink & Remsen 1986). Other possible processes not tested here could explain the pattern observed (e.g. common ancestry) although it would be surprising if *A.l. intensus* and *A.l. yariguierum* were sister populations given that various other *A. lacrymosus* taxa have geographically more proximate distributions.

Species limits.—*A. melanogenys* has been treated as a subspecies of *A. lacrymosus* by some authors (e.g. Hellmayr 1936, Zimmer 1944, Storer 1970, Isler & Isler 1999) or as part of a superspecies together with *A. lacrymosus* (Sibley & Monroe 1990). Our analyses support maintaining species rank for *A. melanogenys* (following, e.g., Meyer de Schauensee 1964, 1966, Hilty & Brown 1986, Fjeldså & Krabbe 1990, Ridgely & Tudor 1994, 2009, Dickinson 2003, Restall *et al.* 2006, Remsen *et al.* 2009, Salaman *et al.* 2009). *A. melanogenys* has a longer bill than *A. lacrymosus*, with a different, more elongated shape (Fig. 1). This measurement is diagnosable to Level 5 from proximate populations, *A.l. melanops*, *A.l. pallididorsalis* and *A.l. tamae* (and *A.l. lacrymosus*), and to Level 2 from other races of *A. lacrymosus*. The tarsus length of *A. melanogenys* is also diagnosable up to Level 3 from geographically proximate *A.l. pallididorsalis*. In contrast, there are no differences beyond Level 2 for any measurements among current *A. lacrymosus* subspecies. In plumage, the combination of a cerulean blue crown and absence of a yellow nuchal 'tear' in *A. melanogenys* involves differences in both pattern and coloration from all *A. lacrymosus* taxa. *A. melanogenys* further lacks strong blue feathering on its rump and has paler yellow underparts, and greener-blue upperparts and remiges compared to *A. lacrymosus* (Fig. 1). *A. melanogenys* calls have a consistently different note shape compared to *A. lacrymosus* populations, being delivered faster and appearing as virtually a straight line (as opposed to an upstroke or up-down stroke) on sonograms (Figs. 5I, 6F). The Santa Marta Mountains are isolated geographically from the Andes and harbour a number of endemic high-elevation birds considered specifically distinct from populations in the Andes (e.g. Krabbe 2008b), of which *A. melanogenys* appears to be an example. In contrast, although various allopatric *A. lacrymosus* taxa constitute phylogenetic species (based on plumage), none are known to occur in sympatry and morphological differences between populations do not approach the differentiation shown between *A. melanogenys* and other taxa. As a result, we recommend maintaining species rank for *A. melanogenys* and *A. lacrymosus*, with no further splits for now, under the Biological Species Concept.

Acknowledgements

We thank the rest of the EBA Project and YARE Project teams, especially Blanca Huertas and also Elkin Briceño, John Arias, Martín Donegan, Cristóbal Ríos, Laura Rosado and Diana Villanueva, and local guides José Pinto, Alonso Masías and Hernando Figueroa. Hernando Guevara (Corporación Autónoma Regional para la Defensa de la Meseta de Bucaramanga—CDMB), Alvaro Prada Prada, Armando Rodríguez and Hector Lamo (CAS), and the mayors of San Vicente de Chucurí, Galán and El Carmen provided the necessary permissions for field work (CAS resolution no. 832). Paul Sweet and Peg Hart (AMNH), Robert Prýs-Jones, Mark Adams and Douglas Russell (BMNH), Enrique Castillo and Fernando Forero (IAVH), José Gregorio Moreno Patiño (UIS), Roque Casallas and Arturo Rodríguez (MLS), F. Gary Stiles (ICN), J. F. Voisin & C. Voisin (MNHN), Oscar Murillo (MHNUV), Gladys Reinoso Flórez, Yair Molina and Mauricio Vejarano (CZUT) and María del Pilar Rivas and Fernando Ayerbe (MHNUC) facilitated access to specimens. Sylke Frahnert (ZMB), Stephen Rogers (CM), Mary Hennen (FMNH), Nathan Rice (ANSP), Paul Sweet and Peg Hart (AMNH) and James Dean (USNM) provided photographs of specimens. Thanks to Biomap Project (especially Juan Carlos Verhelst, Paul Salaman and Andrea Morales) and ProAves (David Caro and Lina Marcela Enriquez) for data and to all of the photographers, recordists and observers mentioned in Appendix 1. Expeditions to Serranía de los Yariguíes received generous financial support from the Royal Geographical Society (with Rio Tinto plc), Duke of Edinburgh, Fondo para Acción Ambiental, Fundación Omacha, Conservation International Colombia (Becas Iniciativa de Especies Amenazadas—Jorge Ignacio “El Mono” Hernández-Camacho), the Percy Sladen Memorial Fund (Linnean Society) and Fundación ProAves. The YARE Project was supported by the BP Conservation Programme (BirdLife International, Conservation International, Flora & Fauna International, Wildlife Conservation Society), Game Conservancy Trust, Fundación ProAves, World Pheasant Association, Universidad Industrial de Santander, Universidad de Caldas, Universidad de Tolima, and Gobernación de Santander. We thank Nate Rice, Robert Bleiweiss and Raúl Sedano for comments on the manuscript. A Robert Giles scholarship from Fundación ProAves, Beca Proyecto Semilla of Universidad de los Andes and Fondo Colombia Biodiversa of Fundación Alejandro Ángel Escobar supported JEA’s field work as part of his graduate studies, and Idea Wild and The Explorers Club’s Exploration Fund assisted with equipment and financial support. Fundación ProAves supported TMD’s work in Santa Marta.

References:

- Álvarez, M., Caro, V., Laverde, O. & Cuervo, A. M. 2007. *Guía sonora de los Andes colombianos*. CDs. Instituto Alexander von Humboldt, Bogotá & Cornell Lab. of Ornithology, Ithaca, NY.
- Álvarez R., M. & Córdoba C., S. 2002. *Guía sonora de las aves del departamento de Caldas, cuencas de los ríos Tapias y Tareas*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva.
- Amadon, D. 1949. The seventy-five per cent rule for subspecies. *Condor* 51: 250–258.
- Bleiweiss, R. 2008. Phenotypic integration expressed by carotenoid-bearing plumages of tanager-finches Thraupini, Emberizinae) across the avian visible spectrum. *Biol. J. Linn. Soc.* 93: 89–109.
- Boesman, P. 1999. *Birds of Venezuela: photographs, sounds and distributions*. CD-ROM. Bird Songs International, Westernieland.
- Burns, K. J. 1998. Molecular phylogenetics of the genus *Piranga*: implications for biogeography and the evolution of morphology and behavior. *Auk* 115: 621–634.
- Burns, K. J. & Naoki, K. 2004 Molecular phylogenetics and biogeography of Neotropical tanagers in the genus *Tangara*. *Mol. Phyl. & Evol.* 32: 838–854.
- Cadena, C. D., Córdoba C., S., Londoño, G. A., Calderón-F., D., Martín, T. E. & Baptiste, M. P. 2007. Nesting and singing behavior of Common Bush-Tanagers (*Chlorospingus ophthalmicus*) in South America. *Orn. Colombiana* 5: 54–63.
- Cracraft, J. 1983. Species concepts and speciation analysis. *Current Orn.* 1: 159–187.
- Dickinson, E. C. (ed.) 2003. *The Howard & Moore complete checklist of the birds of the world*. Christopher Helm, London.
- Donegan, T. M. 2008. Geographical variation in Slate-crowned Antpitta *Grallaricula nana*, with two new subspecies from Colombia and Venezuela. *Bull. Brit. Orn. Cl.* 128: 150–178.
- Donegan, T. M. & Avendaño, J. E. 2008. Notes on tapaculos (Passeriformes: Rhinocryptidae) of the Eastern Andes of Colombia and Venezuelan Andes, with a new subspecies of *Scytalopus griseicollis* from Colombia. *Orn. Colombiana* 6: 24–65.
- Donegan, T. M. & Huertas, B. C. (eds.) 2005. Threatened species of Serranía de los Yariguíes: final report. *Colombian EBA Project Rep. Ser.* 5: www.proaves.org.
- Donegan, T. M. & Huertas, B. C. 2006. A new brush-finch in the *Atlappetes latinuchus* complex from the Yariguíes Mountains and adjacent Eastern Andes of Colombia. *Bull. Brit. Orn. Cl.* 126: 94–116.
- Donegan, T. M., Avendaño-C., J. E., Briceño-L., E. R. & Huertas, B. 2007. Range extensions, taxonomic and ecological notes from Serranía de los Yariguíes, Colombia’s new national park. *Bull. Brit. Orn. Cl.* 127: 172–213.
- Donegan, T., Huertas, B., Avendaño J., Briceño, E. & Donegan, M. 2008. The first biological explorations of Serranía de los Yariguíes, Colombia. *Neotrop. Birding* 3: 38–43.

- Fjeldså, J. & Krabbe, N. 1990. *Birds of the high Andes*. Zool. Mus., Univ. of Copenhagen & Apollo Books, Svendborg.
- Graves, G. R. 1985. Evolutionary correlates of speciation and intraspecific variation in plumage in Andean forest birds. *Auk* 102: 556–579.
- Helbig, A. J., Knox, A. G., Parkin, D. T., Sangster, G. & Collinson, M. 2002. Guidelines for assigning species rank. *Ibis* 144: 518–525.
- Hellmayr, C. E. 1936. Catalogue of birds of the Americas, pt. IX. *Field Mus. Nat. Hist. Publ., Zool. Ser.* 13(9).
- Hilty, S. L. 2003. *Birds of Venezuela*. Princeton Univ. Press.
- Hilty, S. L. & Brown, W. L. 1986. *A guide to the birds of Colombia*. Princeton Univ. Press.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *Intern. J. Climatology* 25: 1965–1978.
- Hubbs, C. L. & Perlmutter, A. 1942. Biometric comparison of several samples with particular reference to racial investigations. *Amer. Naturalist* 76: 582–592.
- Huertas, B. C. & Arias, J. J. 2007. A new butterfly species from the Colombian Andes and a review of the taxonomy of the genera *Idioneurula* Strand, 1932 and *Tamania* Pycrz, 1995 (Lepidoptera: Nymphalidae: Satyrinae). *Zootaxa* 1652: 27–40.
- Huertas, B. C. & Donegan, T. M. (eds.) 2006. Proyecto YARE: investigación y evaluación de especies amenazadas de la Serranía de los Yariguíes, Santander, Colombia. Informe Preliminar Etapa 1. *Colombian EBA Project Rep. Ser. 7*: www.proaves.org.
- International Commission on Zoological Nomenclature (ICZN). 1999. *International code of zoological nomenclature*. Fourth edn. The International Trust for Zoological Nomenclature, c/o The Natural History Museum, London.
- Isler, M. L., Isler, P. R. & Whitney, B. M. 1998. Use of vocalizations to establish species limits in antbirds (Passeriformes; Thamnophilidae). *Auk* 115: 577–590.
- Isler, M. L., Isler, P. R. & Whitney, B. M. 2006. Species limits in antbirds (Thamnophilidae): the Warbling Antbird (*Hypocnemis cantator*) complex. *Auk* 124: 11–28.
- Isler, M. L., Isler, P. R. & Whitney, B. M. 2007. Species limits in the “*Schistocichla*” complex of *Percnostola* antbirds (Passeriformes: Thamnophilidae). *Wilson J. Orn.* 119: 53–70.
- Isler, M. L. & Isler, P. R. 1999. *Tanagers*. Christopher Helm, London.
- Krabbe, N. 2008a. *Birds of the Sierra Nevada de Santa Marta, Colombia*. CDs. John V. Moore Nature Recordings, San Jose, CA.
- Krabbe, N. 2008b. Vocal evidence for restitution of species rank to a Santa Marta endemic: *Automolus rufipectus* Bangs (Furnariidae), with comments on its generic affinities. *Bull. Brit. Orn. Cl.* 128: 219–227.
- Krabbe, N. & Nilsson, J. 2003. *Birds of Ecuador: sounds and photographs*. DVD-ROM. Bird Songs International, Westernieland.
- Krabbe, N., Moore, J. V., Coopmans, P., Lysinger, M. & Ridgely, R. S. 2001. *Birds of the Ecuadorian highlands: the upper montane and páramo zones of Ecuador*. CDs. John V. Moore Nature Recordings, San Jose, CA.
- Krabbe, N., Flórez, P., Suárez, G., Castaño, J., Arango, J. D. & Duque, A. 2006. The birds of Páramo Frontino, West Andes of Colombia. *Orn. Colombiana* 4: 39–50.
- Kroodsma, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. *Auk*, 101: 13–24.
- Meyer de Schauensee, R. 1964. *The birds of Colombia and adjacent areas of South and Central America*. Acad. Nat. Sci., Philadelphia.
- Meyer de Schauensee, R. 1966. *The species of birds of South America and their distribution*. Livingston Publishing, Narberth, PA.
- Moore, J. V. & Lysinger, M. 1997. *The birds of Cabañas San Isidro, Ecuador*. Cassettes. John V. Moore Nature Recordings, San Jose, CA.
- Munsell Color. 1977. *Munsell® color charts for plant tissues*. GretagMacbeth LLC, New York.
- Munsell Color. 2000. *Munsell® soil color charts*. GretagMacbeth LLC, New York.
- Patten, M. A. & Unitt, P. 2002. Diagnosability versus mean differences of Sage Sparrows subspecies. *Auk* 119: 26–35.
- Paynter, R. A. 1982. *Ornithological gazetteer of Venezuela*. Mus. Comp. Zool., Cambridge, MA.
- Paynter, R. A. 1997. *Ornithological gazetteer of Colombia*. Second edn. Mus. Comp. Zool., Cambridge, MA.
- Pearson, R. G., Raxworthy, C. J., Nakamura, M. & Peterson, A. T. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* 34: 102–117.
- Phillips, S. J., Anderson, R. P. & Schapire, R. E. 2006. Maximum entropy modelling of species geographic distributions. *Ecol. Modelling* 190: 231–259.
- Remsen, J. V. 1984. High incidence of “leap-frog” pattern of geographic variation in Andean birds: implications for the speciation process. *Science* 224: 171–173.
- Remsen, J. V., Cadena, C. D., Jaramillo, A., Nores, M., Pacheco, J. F., Robbins, M. B., Schulenberg, T. S., Stiles, F. G., Stotz, D. F. & Zimmer, K. J. 2009. A classification of the bird species of South America (version 15 July 2009). www.museum.lsu.edu/~Remsen/SACCBaseline.html

- Restall, R., Rodner, C. & Lentino, M. 2006. *Birds of northern South America*. Christopher Helm, London.
- Ridgely, R. S. & Tudor, G. 1989. *The birds of South America*, vol. 1. Oxford Univ. Press.
- Ridgely, R. S. & Tudor, G. 2009. *The birds of South America, passerines*. Christopher Helm, London.
- Ridgely, R. S. & Greenfield, P. J. 2001. *The birds of Ecuador*. Cornell Univ. Press, Ithaca, NY.
- Salaman, P., Donegan, T. & Caro, D. 2009. Listado de aves de Colombia 2009. *Conserv. Colombiana* 8: 1–86.
- Sibley, C. G. & Monroe, B. L. 1990. *Distribution and taxonomy of birds of the world*. Yale Univ. Press, New Haven, CT.
- Smithe, F. B. 1975 *Naturalists' color guide*. Amer. Mus. Nat. Hist., New York.
- Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wege, D. C. 1998. *Endemic Bird Areas of the world: priorities for biodiversity conservation*. BirdLife International, Cambridge, UK.
- Stiles, F. G. & Caycedo, P. 2002. A new subspecies of Apolinar's Wren (*Cistothorus apolinari*, Aves: Troglodytidae), an endangered Colombian endemic. *Caldasia* 24: 191–199.
- Storer, R. W. 1970. Subfamily Thraupinae. Pp. 246–408 in Paynter, R. A. (ed.) *Check-list of birds of the world*, vol. 13. Mus. Comp. Zool., Cambridge, MA.
- Strewe, R. & Navarro, C. 2004. The threatened birds of the río Frío Valley, Sierra Nevada de Santa Marta, Colombia. *Cotinga* 22: 47–55.
- Zimmer, J. T. 1944. Studies of Peruvian birds. No. XLVIII: the genera *Iridosornis*, *Delothraupis*, *Anisognathus*, *Buthraupis*, *Compsocoma*, *Dubusia* and *Thraupis*. *Amer. Mus. Novit.* 1262.
- Zink, R. M. 2003. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proc. Roy. Soc. Lond. B* 27: 561–564.
- Zink, R. M. & Renssen, J. V. 1986. Evolutionary processes and patterns of geographic variation in birds. *Current Orn.* 4: 1–69.
- Addresses:* Thomas Donegan, Fundación ProAves, 33 Blenheim Road, Caversham, Reading RG4 7RT, UK, e-mails: tdonegan@proaves.org / thomasdonegan@yahoo.co.uk. Jorge E. Avendaño, Departamento de Ciencias Biológicas, Universidad de los Andes, A.A. 4976, Bogotá, Colombia, e-mails: je.avendan0955@uniandes.edu.co / jorgeavec@gmail.com

APPENDIX 1: Materials examined

Specimen data are organised alphabetically by museum, then in number order by specimen number. Other data are organised from south to north. Elevations are only presented when given on specimen labels and, if given in feet, have been converted to metres. Assignment of specimens or observations to subspecies in the Central Andes is based upon arbitrary segregation between (i) Central Andean populations of *A.l. palpebrosus* and *A.l. olivaceiceps* near the Caldas–Antioquia border (c.05°30'–06°00'N), where there is a gap in records; and (ii) between *A.l. palpebrosus* and *A.l. caeruleascens* at the latitude of the southern Tungurahua border (c.01°30'S) in central Ecuador.

Specimens

The following museum codes are used in this section. Museums marked * were visited by the authors, with other specimen data from Biomap, which were confirmed with photographs in instances noted below. AMNH* = American Museum of Natural History, New York, USA. ANSP = Academy of Natural Sciences, Philadelphia, USA. BMNH* = Natural History Museum, Tring, UK. CM = Carnegie Museum of Natural History, Pittsburgh, USA. CMUC = Centro de Museos, Universidad de Caldas, Manizales, Colombia. COP = Colección Ornitológica Phelps, Caracas, Venezuela. CZUT* = Colección Zoológico, Universidad de Tolima. FMNH = Field Museum of Natural History, Chicago, USA. FVZ = Western Foundation of Vertebrate Zoology, Caramillo, USA. IAVH* = Instituto Alexander von Humboldt, Villa de Leyva, Colombia. ICN* = Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia. INCIVA = Instituto Vallecaucano de Investigaciones, Cali, Colombia. LACM = Los Angeles County Museum of Natural History, Los Angeles, USA. LSU = Museum of Natural Science, Louisiana State University, Baton Rouge, USA. MCSJ = Museo Colegio San José, Universidad de la Salle, Medellín, Colombia. MHNNL = Muséum d'Histoire Naturelle de Neuchâtel, Neuchâtel, Switzerland. MLS* = Museo de la Universidad de la Salle, Bogotá, Colombia. MNHN* = Muséum Nationale d'Histoire Naturelle, Paris, France. MHNG = Muséum d'Histoire Naturelle de Genève, Geneva, Switzerland. MHNUV* = Museo de Historia Natural, Universidad de Valle, Cali, Colombia. MHNUC* = Museo de Historia Natural, Universidad del Cauca, Popayán, Colombia. MVZ = Museum of Vertebrate Zoology, University of California, Berkeley, USA. UMMZ = Museum of Zoology, University of Michigan, Ann Arbor, USA. SMF = Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany. USNM = Smithsonian Institution, National Museum of Natural History, Washington, USA. YPM = Peabody Museum of Natural History, Yale University, USA. ZMB = Museum für Naturkunde der Humboldt Universität, Berlin, Germany. ZSM = Zoologische Staatssammlung, München, Germany.

A. melanogenys SANTA MARTA, COLOMBIA: AMNH 72429, 72481–85 (El Líbano, Magdalena, 11°10'N, 74°00'W), 72479–80, 72486–88 (San Lorenzo, Magdalena, 11°10'N, 74°07'W); BMNH 1885.6.7.29 (Templado,

Valledupar, Cesar, 1,981 m, 10°33'N, 73°29'W), 1885.6.7.30–31 ('nr. San Sebastián' [de Rabago, Valledupar, Cesar], 10°34'N, 73°36'W); CM 29072 (San Lorenzo, as above, photograph); ICN 2168–69, 23466–72, 23474, 23476–78, 23480–83 (San Lorenzo, as above), 23484 (Cuchilla Cebolleta, Ciénaga, Magdalena, 10°55'N, 73°55'W); MNHN 6406 / CG1932 / 1340 ('Santa Marta'). *Biomap*: ANSP 63234–38, 184423 (San Miguel, Dibulla, La Guajirá, 10°58'N, 73°29'W); CM 8820, 8826 (El Líbano, as above), 37800–02, 37919, 37942, 37959–60, 37971, 37984–85, 42541, 102869–70 (San Lorenzo, as above), 38642–45, 38662, 39659 ('Santa Marta'), 45042 (Alto de Chirua, Riohacha, La Guajirá, 10°56'N, 73°22'W), 45072–73, 45084 (río Macotama, Dibulla, La Guajirá, 10°55'N, 73°30'W); FMNH 72773–74 (San Lorenzo, as above); LSU 90464–65 (San Lorenzo, as above); MCZ 106392–93, 106395–99, 106401–05, 106407–09 (Macotama, as above); SMF 59900 (San Lorenzo, as above), 72484 (El Líbano, as above); USNM 170370–01 (Macotama, as above), 346926, 388186–87 (Chenducua, Valledupar, Cesar, 10°47'N, 73°25'W), 375135, 388197–202, 388204–05 ('Santa Marta'), 384373–80, 388184–85 (San José, Valledupar, Cesar, 10°45'N, 73°24'W), 388181–83 (río Guatapuri, Valledupar, Cesar, 10°53'N, 73°32'W), 388188 (Cerro el Mamón, Valledupar, Cesar, 10°37'N, 73°33'W), 388191–96 (Chinchicua, Puerto Bello, Cesar, 10°26'N, 73°43'W), 388296, 388207–10 (Siminchucua, Aracataca, Magdalena, 10°40'N, 73°38'W).

A.l. pallidorsalis SERRANÍA DE PERIJÁ, VENEZUELA: AMNH 55591 (Cerro Tetarí, Zulia, Perijá, 10°02'N, 73°02'W, 2,900 m); COP 55586–602 (Cerro Tetarí, as above, all paratypes), 55603–10 (Cerro Pejochaina, Zulia, summit and east slope, 09°57'N, 72°58'W, 2,000–2,300 m, all paratypes), 58118 (Pie Cerro, Zulia, 10°00'N, 72°50'W, 2,350 m), 58119–20 (Campamento Avispa, Zulia, 10°10'N, 72°48'W, 2,175 m), 73026–37 ('Camp Frontera 2', Zulia, 3,000 m, coordinates unknown). COLOMBIA: ICN 36239 (Sabana Rubia, Manaure, Balcón de Cesar, 10°22'N, 72°55'W); 35859, 36042 (Casa de Hierro, Sabana Rubia, La Paz, Cesar, 10°22'N, 72°54'W, 3,400 m); 36727, 36781 (Fig. 2vi) (above El Cinco, La Paz, Cesar, 10°22'N 72°57'W, 2,450 m); 36828, 36830–01, 36835–37, 36846 (Casa de Vidrio, Sabana Rubia, La Paz, Cesar, 10°22'N, 72°54'W, 3,025 m). *Biomap*: FVZ 11852–53 (San Alberto, Cesar, 07°45'N, 73°23'W, but presumably higher than this locality or incorrectly labelled); USNM 375136–44, 375146–52 ('Serranía de Perijá', Cesar / La Guajira)

A.l. melanops CORDILLERA DE MÉRIDA, VENEZUELA: AMNH specimens inspected but no details taken; BMNH 85.6.7.28, 1915.3.1.139–46, 1969.52.90 ('Mérida'), 1969.39.83–84 (Culata, Mérida, 08°45'N, 71°05'W); COP 4737 (Vallecito, Mérida, 08°39'N, 71°06'W, 2,000 m), 5112–16 (Páramo Misisí, Trujillo, 09°20'N, 70°20'W, 2,100 m), 9468–72 (Páramo Zumbador, Táchira, 08°00'N, 72°05'W, 2,500–2,600 m), 14283–91 (Llano Rucio, Mérida, 09°00'N, 71°05'W, 2,500 m), 14595–97 (El Escorial, Mérida, 08°38'N, 71°05'W, 2,800 m), 14699 (Páramo San Antonio, Mérida, 08°40'N, 71°03'W, 3,000 m), 20084–89, 20092–98 (Páramo Cendé, Trujillo, 09°28'N, 70°05'W, 2,700–2,900 m), 20090–91 (Páramo Jabón, Trujillo, 3,000 m, apparently near Páramo Misisí, above, but coordinates unknown), 20279 (El Rincón, Cerro Niquitaz, Trujillo, 09°07'N, 70°30'W, 2,600 m), 24573–77, 24671–72 (Boca de Monte, Pragonero, Táchira, 08°01'N, 71°46'W, 2,300–2,400 m), 45464–79 (El Muerto, north slope, Páramo Aricagua, Mérida, 08°20'N, 71°11'W, 2,900–3,000 m), 49438–48 (La Honda, Santo Domingo, Mérida, 2,700 m, coordinates unknown), 64402–09 (Páramo La Negra, Mérida, 08°15'N, 71°40'W, 3,000–3,200 m), 71587 (Los Arangures, 35 km south of Mucuchíes, Mérida, 2,890 m, coordinates unknown); MNHN 3193–95, one unnumbered ('Mérida').

A.l. tamae EASTERN CORDILLERA, VENEZUELA: AMNH 11244 (Páramo Tamá camp, 07°25'N, 72°26'W, 3,000 m); COP 11241–48 (Páramo Tamá camp, as above, 2,000–3,000 m, all paratypes), 61517–21, 62505–15 (Hacienda La Providencia, río Chiquito, Táchira, 07°38'N, 72°12'W, 1,800–2,300 m), 74095–106 (Cumbre Cerro Retiro, Rebancha, Táchira, coordinates unknown, 2,800 m). COLOMBIA: AMNH 513795 ('Colombia'); CM 60221 (Boca del Monte, Boyacá, possibly c.05°36'N, 72°27'W but not included in analysis, photograph); FMNH 261868–70 (Hacienda la Primavera, Cubará, Boyacá, 07°00'N, 72°20'W) (photograph); ICN 18191 (Fig. 2v), 18192 (Toledo, Páramo de Tamá, Norte de Santander, 07°19'N, 72°28'W); MLS 5794, 6760–64 (Fontibón, Pamplona, Norte de Santander, 07°21'N, 72°39'W); USNM 410162 (Pamplona, Norte de Santander, 07°23'N, 72°39'W) (photograph).

A.l. olivaceiceps WESTERN CORDILLERA, COLOMBIA: AMNH 134366–70, 134374–76, (Paramillo, Antioquia, 07°03'N, 75°55'W); BMNH 1921.12.29.48 (Paramillo, as above); ICN 35001 (Fig. 2iii) (Vereda Monserrate, Jardín, Antioquia, 05°37'N, 75°53'W). *Biomap*: USNM 256357, 436971–75, 436977–78, 436980 (Paramillo, as above), 436966 (Hacienda La Ilusión, Urrao, Antioquia, 06°25'N, 76°05'W). CENTRAL CORDILLERA, COLOMBIA: AMNH 40703 ('Bogotá'); 148083 (Sabanalarga, Antioquia, 06°51'N 75°48'W), 513792 (Santa Elena, Antioquia, 06°15'N, 75°35'W), 513793–94 (both 'Medellín'); ANSP 7375 ('Bogotá', photograph); BMNH 85.6.12.417 ('Bogotá'), 1885.6.7.23–25, 1885.6.12.419 (Santa Elena, as above); ICN 34345, 34465 (El Escobero, San Sebastián, Envigado, Antioquia, 06°10'N, 75°35'W); ZMB 15879 ('New Granada', photograph); MLS 4826 (San Pedro, Antioquia, 06°28'N, 75°33'W), 4827 (Yarumal, Marconi, Antioquia, 06°58'N, 75°24'W), 8193 (El Chaquiro, Santa Rosa, Antioquia, 06°45'N, 75°32'W); MNHN al01, CG1999.3198 ('Antioquia'). *Biomap*: MCSJ 144 (San Pedro, as above), 284 (Boquerón, Antioquia, 06°17'N, 75°37'W), 480A, 481A, 482 (Santa Elena, as above), 2805 (Páramo de Sonsón, Antioquia, 05°43'N, 75°15'W), 2928–29, 2931 (Belmira, Páramo Santa Inés, Antioquia, 06°48'N, 75°43'W); MHN NL 92.8759, 92.8760A, 92.8760B ('Medellín'); USNM 427569–77, 428069, 536578 (Santa Rosa de Osos, Antioquia, 06°39'N, 75°28'W), 428068 ('Antioquia'), 436967–70 (Sonsón, Antioquia, 05°42'N, 75°18'W).

A.l. palpebrosus COLOMBIA: AMNH 40703 ('Bogotá'); 117339–42 (Almaguer, Cauca, 01°55'N, 76°50'W), 112988 (río Toche, Ibagué, Tolima, 04°32'N, 75°25'W), 112989 (Páramo de Santa Isabel, Risaralda / Tolima / Caldas border, 04°47'N, 75°26'W); 112991, 112993–3002 (Laguneta, Quindío, 04°34'N, 75°30'W); BMNH 1885.6.12.418 ('New Grenada'); CZUT 497, 505 (La Cascada, Anzoátegui, Tolima); ICN 2810 (San Marcos, Cauca, 02°20'N, 76°05'W), 2811–12 (Paletará, Cauca, 02°10'N, 76°26'W), 2813 (Termales, Tolima / Caldas, 04°58'N, 75°23'W), 2814 (Palermo, San Juan, Huila, 02°53'N, 75°28'W), 2815–16 (Fig. 2i) (La Cocha, Pasto, Nariño, 01°05'N, 77°09'W), 8502, 8531 (Chorroado, Puerres, Nariño, 00°50'N, 77°25'W), 26145, 26150, 26152–53, 26157 (Parque Nacional Natural (PNN) Nevado del Huila, Páez, Cauca, 03°01'N, 76°00'W), 29230, 29263, 29268, 29277–78 (La Victoria, Tumaco / Ipiales, Nariño, 00°35'N, 77°10'W), 29339 (Llorente, Nariño, 00°49'N, 77°15'W), 20445 (Herbeo, Tolima, 05°05'N, 75°20'W); MHNUC 2440–41, 2445–46, 2449 (La Victoria, as above), 2442 (Paletará, as above), 2444 (Muluzua, Totoró, Cauca, 02°29'N, 76°18'W); MHNUV 4435–38 (Bosque del Oso, 1.5 hours from Hacienda Corinto, Villa María, Caldas, coordinates unknown); 4862–63 (Finca Bengala, 3 km north of Cocora at the end of the Salento–Cocora, Salento, Quindío, 04°38'N, 75°29'W), 4563–64 (Bosque del Alto del Dulce, El Provenir / Bernal, road to Villamaría, Santa Rosa de Cabal, Risaralda, 04°52'N, 75°38'W), 4861, 5880–81 (km 33, Carretera Paletará–San José de Isnos, 1 km east of Quebrada Bujías, Huila, 02°00'N, 76°17'W); USNM 81823–24 ('Colombia', photographs). *Biomap*: ANSP 7374 (Pasto, Nariño, 01°13'N, 77°17'W), 162197, 162201–02, 162204 (Chorroado or Puerres, as above), 162198–99 (Derrumbe, Nariño, presumably at higher elevation than this locality, coordinates unknown), 162205–07, 162209–10 (Páramo de Guamués, as above), 154485–90, 154492–94, 154496 (Laguneta, as above); CM 26100, 70261–62, 70346, 70412, 70426 (Zacudo, Manizales, Caldas, 05°05'N, 75°30'W); CMUC 226 (Parque Regional Ucumari, Risaralda, 04°39'N, 75°36'W), 341AE (Páramo de Letras, Caldas, 05°10'N, 75°20'W); FMNH 226920–21 (Moscopán, Cauca, 02°20'N, 76°05'W), 251435 (El Crucero, Puracé, Cauca, 02°20'N, 76°39'W), 255809 (San Rafael, Puracé, Cauca, 02°25'N, 76°25'W), 288119–22, 288139–40, 288152, 399532–33, 399539–44 (La Victoria, as above); ZSM 1965.391–93, 1965.522, 1965.525 (Totoró, as above), 1965.523–24 (Santa Leticia, La Plata, Huila, 02°14'N, 76°10'W); INCIVA 2502 (Reserva Natural (RN) La Planada, Ricaurte / Barbacons, Nariño, 01°15'N, 78°15'W), 2508, 2510 (Totoró, as above), 2509 (10 km north of Pasto, Nariño, 01°14'N, 77°17'W), 2511 (Coconuco, PNN Puracé, Cauca, 02°24'N, 76°27'W); LSU 38935–36 (Totoró, as above), 48194, 61902 (El Crucero, as above); MHNG 1179.076–078, 1179.080–081 (La Victoria, as above); MVZ 120670 (3 km east of Andalucía, Huila, 01°54'N, 75°41'W), 140719 (Cordillera de Portachuelo, Putumayo, 01°07'N, 76°52'W), 223291 (río Toche, as above); UMMZ 223290 (Páramo de Guamués, Nariño, 00°50'N, 77°20'W), 223292 (Laguneta, as above); LACM 39723, 39735 (Conocuno, as above), 33247–50, (Totoró, as above), 33251–52 (La Plata, as above); USNM 447616–21 (Puracé, Cauca, presumably as above); YPM 32195 (Totoró, as above). ECUADOR: AMNH specimens inspected but no details taken; BMNH 1847.1.16.15 (no locality data), 1860.11.26.24 ('Quito'), 1885.6.7.26–27 (Villagómez, San Lucas), 1925.12.24.244, 1925.12.24.278 (Huila), 1938.12.20.121 (Papallacta), 1940.12.5.183–184 (Cuyuja, Napo / Pastaza), 1969.52.88–89 (below Papallacta). Specimens labelled *A.l. caeruleus* ECUADOR: AMNH specimens inspected but no details taken; BMNH 1953.68.412 (Huaico, Loja). PERU: AMNH specimens inspected but no details taken; BMNH 1885.6.8.435 (Cutervo).

A.l. intensus WESTERN CORDILLERA, COLOMBIA: AMNH 110213–24, 110227–30 ('Coastal range', Cauca, coordinates unknown but presumably near Munchique), 461665 (Cerro Munchique, Cauca, see below); ICN 25790 (Fig. 2ii), 25818 (Farallones del Cauca, Valle del Cauca, 03°22'N, 76°45'W), 25864, 30107 (Chargüayaco, Cerro Munchique, El Tambo, Cauca, 02°40'N, 76°57'W); MHNUC 2443 (Chargüayaco, as above), 3375–77 (La Romelia, PNN Munchique, El Tambo, Cauca, 02°27'N, 76°49'W); MHNUV 1048 (río Cali, Calle, 2,000–2,300 m, 03°30'N, 76°30'W) 3926, 3929, 3940, 3995, 4005, 4006 (Alto del Buey, Farallones de Cali, as above) 4563–64 (Bosque de Alto del Dulce–El Porvenir, Santa Rosa de Cabral, Risaralda); MLS 6765–66 (El Tambo, as above). *Biomap*: ANSP 141900, 141902–03, 144630 (Munchique, as above), 141905, 150225 (Gamboá, San Antonio, Cauca, 02°37'N, 76°54'W); FMNH 53776–77, 307939 (west of Popayán, Cauca, no details), 226916–17, 249986–89 (Munchique, as above); LSU 38934 (Munchique, as above); MHNG 1140.017–22, 1167.045, 1216.028 (Munchique, as above); LACM 29247–57, 37576 (Munchique, as above); USNM 459541–46 (El Tambo, as above); YPM 32196–97 (Munchique, as above).

A.l. lacrymosus PERU: AMNH: all specimens inspected and seven measured but no details taken; BMNH 1896.10.6.168, 1896.10.6.169 (latter, two specimens, same no.) (Chachapoyas, 2,743 m), 1885.6.12.421 (Higos); MNHN 3196, GC1901in1676 (Cumpary, 2,400 m).

Photographs

A.l. melanops CORDILLERA DE MÉRIDA, VENEZUELA: PNN Dinira, Lara, 09°34'N, 70°06'W (J. E. Miranda T.: Fig. 1vi).

A.l. yariguierum SERRANÍA DE LOS YARIGUÍES, COLOMBIA: Lepipuerto (details in text) (Donegan *et al.* 2007).

A.l. olivaceiceps WESTERN CORDILLERA, COLOMBIA: Reserva Natural de Aves (RNA) Colibrí de Sol, Urrao, Antioquia, 06°26'N, 76°05'W, 3,400 m (Krabbe *et al.* 2006; A. Quevedo / ProAves: Fig. 1(iv)).

CENTRAL CORDILLERA, COLOMBIA: La Lana, San Pedro de los Milagros, Antioquia, 06°27'N, 75°36'W, 2,645 m (T. M. Donegan / J. E. Avendaño / B. Huertas: Fig. Iiii).

A.l. palpebrosus COLOMBIA: Reservas de Aves Comunitarias, Roncesvalles, Tolima, 04°00'N, 75°40'W (A. Quevedo / ProAves: Fig. 1v); RNA Loro Coroniazul y El Mirador, Génova, Quindío, 04°08'N, 75°44'W, 3,200 m (A. Quevedo / ProAves).

A.l. intensus WESTERN CORDILLERA, COLOMBIA: RNA Mirabilis-Swarovski, Cauca, 02°31'N, 76°59'W, 2,400 m (J. P. López Ordoñez / ProAves: Fig. 1vii).

Sound-recordings

A. melanogenys SANTA MARTA, COLOMBIA: RN El Dorado, San Lorenzo, Magdalena, 11°06–09'N, 74°03–06'W, 1,450–2,700 m (Krabbe 2008a: Fig. 6F; C. Hesse recording: XC 10194; T. M. Donegan recording: XC 37290).

A.l. pallidioralis SERRANÍA DE PERIJÁ, COLOMBIA: above El Cinco, vereda El Cinco, Manaure, Cesar, 10°21'N 72°56'W, 2,450 m (J. E. Avendaño: Fig. 6D).

A.l. melanops CORDILLERA DE MÉRIDA, VENEZUELA: Parque Nacional (PN) Guaracamal, Trujillo, 09°10'N, 70°11'W (Boesman 1999: Fig. 6C).

A.l. yariguierum SERRANÍA DE LOS YARIGUÍES, COLOMBIA: Lepipuerto (details in text).

A.l. olivaceiceps CENTRAL CORDILLERA, COLOMBIA: Bello, San Félix, Serranía Las Baldías, Antioquia, 06°01'N, 75°35'W (Álvarez *et al.* 2007: Fig. 5F).

A.l. palpebrosus COLOMBIA: San Juan de Pasto, Daza, Nariño, 01°16'N, 76°15'W, 2,800 m (O. Laverde: XC 12748–49: Figs. 5G, 5H); río Blanco, Caldas, 05°05'N, 75°21'W (Álvarez *et al.* 2007: Fig. 6E); Neira, vereda la Cristalina, headwaters of the río Tapias, Caldas, supposedly 05°34'N 74°53'W but probably further west and at higher elevation (Álvarez & Córdoba 2002, Álvarez *et al.* 2007: Fig. 5C). ECUADOR: Cordillera de Güacamayos, Napo, 00°37'S, 77°50'W, 2,300 m (Krabbe *et al.* 2001; Krabbe & Nilsson 2003); Cabañas San Isidro, Napo (00°35'S, 77°53'W, 2,100 m) (Moore & Lysinger 1997); Guango Lodge, Napo, 00°23'S, 78°36'W, 2,800 m (S. Olmstead: XC: 177719); 1 km below Oyacachi, Napo, 00°13'S, 78°04'W, 3,150 m (Krabbe & Nilsson 2003); El Chorillo, Santa Barbara–La Bonita Road, Sucumbíos, 00°36'N, 77°31'W, 2,650 m (Krabbe & Nilsson 2003).

A.l. caerulescens ECUADOR: Reserva Tapichalaca, Zamora-Chinchipec, 04°29'S, 79°09'W and 04°30'N, 79°08'W, 2,500–2,830 m (Krabbe & Nilsson 2003: Fig. 5D; A. Spencer: XC 17470); Cerro Toledo, east slope, Zamora-Chinchipec, 04°23'S 79°06'W, 3,150 m (Krabbe *et al.* 2001; Krabbe & Nilsson 2003); PN Podocarpus, Cajanuma, Loja, 04°06'S 79°09'W and 04°07'S, 79°10'W, 2,750–2,800 m, (Krabbe *et al.* 2001: Fig. 5G; C. Vogt: XC 16408); Gualaceo–Limón road, Morona-Santiago, 03°02'S, 78°35'W (Krabbe *et al.* 2001).

A.l. lacrymosus PERU: Bosque Unchog, Huánuco, 09°41'S, 76°07'W, 3,250 m (C. Hesse: XC 10778, 10779).

Mist-net data

A. melanogenys SANTA MARTA, COLOMBIA: RNA El Dorado (details above) (E. Rodríguez, D. Velasco, C. Olaciregui *et al.* / ProAves).

A.l. yariguierum SERRANÍA DE LOS YARIGUÍES, COLOMBIA: The following individuals were photographed and ringed with ProAves rings, but are not assigned as types: Lepipuerto captures (2): ProAves ring nos. C02480 and C02481, each captured on 9 January 2005 at 07.00 h; Filo Pamplona captures (ten in addition to the recaptured paratype, all with blood samples taken and deposited at UniAndes): C02767 captured on 11 July 2005 at 17.00 h (recaptured on 13 July 2005 at 07.30 h); C02769 captured on 12 July 2005 at 07.00 h; C02770–73 and C02775, all captured on 12 July 2005 at 16.30–17.30 h; C02779 captured on 13 July 2005 at 06.30 h (recaptured on 14 July 2005 at 07.00 h); C02789 captured on 13 July 2005 at 18.30 h; C02791 captured on 14 July 2005 at 07.00 h. For localities, see text.

A.l. olivaceiceps WESTERN CORDILLERA, COLOMBIA: RNA Loro Orejamarillo, Jardín, Antioquia, four localities: 05°32'N, 75°48'W, 2,700 m; 05°33'N, 75°48'W, 2,700 m; 05°36'N, 75°51'W, 1,600 m; 05°46'N, 75°58'W, 1,600 m (G. Suárez *et al.*: ProAves); Páramo Frontino, Antioquia, two localities: 06°26'N, 76°05'W, 3,500 m; 06°25'N, 76°04'W, 2,800 m (D. Carantón *et al.*: ProAves).

A.l. palpebrosus COLOMBIA: Reservas Comunitarias de Roncesvalles, Tolima, 04°00'N, 75°40'W, 1,500–3,500 m (D. Vesasco *et al.*: ProAves); RNA Loro Coroniazul y El Mirador, Mirador, Génova, Quindío, details above (D. Ramirez, F. Guzman *et al.*: ProAves); vereda El Páramo, Marulanda, Caldas, 05°17'N, 75°16'W, 2,800 m (A. Quevedo: ProAves); RN Ibanasca, Tolima, 04°38'N, 75°19'W, 2,900–3,600 m (D. Bejarno / A. González: ProAves); vereda Las Sabinas, Manizales, Caldas (coordinates unknown) (A. Quevedo: ProAves).

Observations

Note: localities mentioned in previous sections are not repeated here.

A. melanogenys SANTA MARTA, COLOMBIA: río Frío, Ciénaga, Magdalena, 10°54'N, 73°53'W, 1,500–2,900 m (Strewe & Navarro 2004).

A.I. pallididorsalis SERRANÍA DE PERIJÁ, COLOMBIA: Cerro Pintado, Cesar, 10°28'N, 72°55'W, 1,500–3,200 m (P. Salaman: ProAves; IAVH).

A.I. yariguierum SERRANÍA DE LOS YARIGÜES, COLOMBIA: Cerro Las Tetas, Camino del Lenguerke, San Vicente de Chucurí, Santander, 06°51'N, 73°21'W (J. C. Luna: ProAves).

A.I. tamae EASTERN CORDILLERA, COLOMBIA: Quetame, Cundinamarca, 04°18'N, 73°52'W (P. Salaman: ProAves); El Alto del Tigre, El Calvario, Meta, 04°22'N, 73°40'W (F. G. Stiles); Loma La Aurora, Bogotá, Cundinamarca, 04°47'N, 74°01'W (P. Salaman: ProAves); Santuario de Fauna y Flora Igüaque, Boyacá, 05°40'N, 73°27'W (J. Zuluaga); Páramo de Monsalve, Santander (07°24'N, 72°56'W, 2950 m) (Avendaño 2006).

A.I. olivaceiceps WESTERN CORDILLERA, COLOMBIA: PNN Tatamá, Pueblo Rico, Risaralda, 05°09'N, 76°02'W (DATAVES). CENTRAL CORDILLERA, COLOMBIA: Páramos del Sur de Antioquia, Antioquia, 05°38'N, 75°12'W, 800–3,200 m (IAVH); Carretera Caldas–Agelópolis, Angelópolis, Antioquia, 06°05'N, 75°39'W, 1,800–2,600 m (P. Restrepo: DATAVES); quebrada El Viao, Cocorná, Antioquia, 06°01'N, 75°27'W, 1,880–1,950 m (DATAVES); Retiro, Antioquia, 06°04'N, 75°30'W, 1,600 m (various observers: DATAVES); Alto del Escobero / San Sebastián, Retiro, Antioquia, 06°03'N, 75°35'W (many observers: DATAVES); Corregimiento San Cristóbal, Medellín, Antioquia, 06°04'N, 75°30'W (M. J. Peña: DATAVES); Cuenca Quebrada, Santa Elena, Medellín, Antioquia, coordinates as above (G. J. Castaño: DATAVES); Área de Reserva Forestal Protectora, La Romera, Sabaneta, Antioquia, 06°07'N, 75°36'W (P. Pulgarín: DATAVES); Envigado, Antioquia, 06°09'N, 75°36'W (R. Vélez de Bedout: DATAVES); La Estrella, Antioquia, 06°09'N, 75°39'W (A. M. Castaño: DATAVES); Las Antenas, San Félix, Medellín, Antioquia, 06°20'N 75°39'W (many observers: DATAVES); Páramo de Belmira, Belmira, Antioquia, 06°30'N, 75°45'W (T. Cuadros: DATAVES).

A.I. palpebrosus COLOMBIA: Ipiales, Nariño, 00°50'N, 77°37'W (P. Salaman: ProAves); laguna de la Cocha, Pasto, Nariño, 01°07'N, 77°16'W (F. G. Stiles: DATAVES; IAVH); Reserva la Rejoya, Colón, Putumayo, 01°08'N, 76°56'W, 2,660 m (DATAVES); Pasto–Mocóa road, Nariño, coordinates not known (P. Salaman: ProAves); Coconuco; Daza, Pasto, Nariño, 2,800 m, 01°17'N, 77°15'W (C. Downing); Serranía de las Minas, Huila, 02°10'N, 76°11'W, 2,100–2,700 m (IAVH); Reserva Natural Privada Meremberg, La Plata, Huila, 02°23'N, 76°23'W, 2,200–2,400 m (P. Salaman: ProAves; P. Flórez: DATAVES); PNN Puracé, Cauca, 02°22'N, 76°30'W, 2,600–2,800 m (P. Flórez & F. Piedrahita: DATAVES); Pilimbala–San Nicolás road, PNN Puracé, Cauca, coordinates unknown (P. Salaman: ProAves); cuenca del río Hereje, Tolima, 03°18'N, 76°00'W, 3,280–3,760 m (IAVH); Coconuco–San Agustín road, PNN Puracé, Cauca, coordinates unknown (P. Salaman: ProAves); Reserva Natural Semillas de Agua, Tolima, 04°14'N, 75°33'W, 3,100–3,800 m (IAVH); Reserva Natural Privada Semillas de Agua, Cajamarca, Tolima, 04°27'N, 75°26'W (Querubín Rodríguez Pinilla: DATAVES); cañón del río Combeima, Tolima, 04°32'N, 75°18'W, 1,700–2,800 m (IAVH); cuenca del río Toche, Tolima, 04°36'N, 75°24'W, 1,500–3,500 m (IAVH); valle del Cocora, Salento, Quindío, 04°37'N, 75°27'W (J. C. Saenz & J. Ramírez: DATAVES); Acaime, RN Alto Quindío, Salento, Quindío, 04°37'N, 75°28'W, 2,500–3,500 m (various observers: DATAVES / ProAves); Serranía de los Paragüas, Quindío, 300–2,700 m (IAVH); Estación Altamira, Reserva Natural Privada Narvaco, Salento, Quindío, 04°38'N, 75°29'W (F. G. Stiles: DATAVES); PNN Ucumarí, Pereira, Risaralda, 04°38'N, 75°35'W (many observers: DATAVES); La Montaña, Reserva Natural Narcavo, Salento, Quindío, 04°38'N, 75°28'W, 2,700 m (D. Duque Montoya / F. G. Stiles: DATAVES); lagunas Bombona and Vancouver, Tolima, 04°39'N, 75°13'W, 3,010–4,000 m (IAVH); La Pastora, Ucumarí, Risaralda, 2,600–2,800 m, 04°42'N, 75°30'W (C. Downing); Finca Paragüay, Santa Isabel, Tolima, 04°45'N, 75°17'W, 3,280–3,760 m (IAVH); Bosques del Oriente de Risaralda, Risaralda, 04°47'N, 75°32'W, 1,800–3,800 m (IAVH); Termales del Ruiz, Villamaría, Caldas, 04°58'N, 75°23'W, 2,800–3,000 m (L. Arango: DATAVES); río Blanco, Manizales, Caldas, 05°04'N, 75°32'W, 2,500 m (many observers: DATAVES, ProAves, IAVH); Marulanda, Caldas, 05°17'N, 75°16'W (L. Rosselli: DATAVES); Pácora, Caldas, 05°32'N, 75°26'W (D. Piedrahita Thiriez: DATAVES). ECUADOR: Additional localities for this and *A.I. caeruleus* listed in Zimmer (1944) and Ridgely & Greenfield (2001).

A.I. intensus WESTERN CORDILLERA, COLOMBIA: El Tigrillo, Munchique, Cauca (J. Sandoval: ProAves); Reserva Natural Tambito, 20 de Julio, Cauca, 02°31'N, 76°59'W, 2,300 m (J. Sandoval: ProAves); Bosque de San Antonio, km 18, east slope of West Andes, Cali, Valle del Cauca, 03°30'N, 76°38'W (C. M. Wagner).

APPENDIX 2: Biometrics of *Anisognathus* taxa

The data below are taken from specimens, or live individuals, by the authors, or other researchers, using the same methodology. For all taxa, data are presented in the form mean \pm standard deviation (n = sample number), with all measurements in mm, except mass (g). / = no data available.

Taxon	Wing-chord (mm)	Tail (mm)	Tarsus (mm)	Bill (to skull) (mm)	Mass (g)
<i>A. melanogenys</i> (Santa Marta, Colombia) specimens	88.2 \pm 3.4 (81.0–94.0) ($n=12$)	73.8 \pm 2.8 (69.0–78.0) ($n=12$)	27.4 \pm 1.0 (26.0–29.0) ($n=12$)	18.5 \pm 0.5 (18.0–19.5) ($n=11$)	/
<i>A. melanogenys</i> (Santa Marta, Colombia) live birds	87.5 \pm 2.9 (84.0–97.0) ($n=20$)	/	/	/	40.5 \pm 3.0 (33.8–44.7) ($n=19$)
<i>A. lacrymosus pallididorsalis</i> (Perijá, Colombia / Venezuela) specimens	89.3 \pm 3.5 (85.0–93.0) ($n=4$)	70.3 \pm 3.4 (67.0–75.0) ($n=4$)	24.3 \pm 0.5 (24.0–25.0) ($n=4$)	14.3 \pm 0.5 (14.0–15.0) ($n=4$)	32.0 ($n=1$)
<i>A.I. melanops</i> (Mérida, Venezuela) specimens	87.9 \pm 2.8 (84.0–92.0) ($n=16$)	70.6 \pm 2.7 (66.0–75.0) ($n=15$)	25.7 \pm 0.9 (24.5–28.0) ($n=15$)	15.9 \pm 0.5 (15.0–16.5) ($n=16$)	/
<i>A.I. yariguierum</i> (Yariguíes, Colombia) live birds	93.7 \pm 4.8 (86.0–101.0) ($n=13$)	74.2 \pm 2.8 (70.0–80.0) ($n=13$)	26.1 \pm 1.1 (24.0–28.3) ($n=13$)	16.1 \pm 1.0 (14.1–17.0) ($n=12$)	35.9 \pm 1.9 (32.5–40.3) ($n=13$)
<i>A.I. yariguierum</i> (Yariguíes, Colombia) specimens	92.6 \pm 4.5 (86.3–99.0) ($n=6$)	78.3 \pm 2.8 (74.1–81.4) ($n=6$)	26.0 \pm 0.4 (24.1–26.5) ($n=6$)	16.7 \pm 0.5 (14.5–17.4) ($n=6$)	35.8 \pm 2.4 (32.0–38.0) ($n=6$)
<i>A.I. tamae</i> (East Andes, Colombia / Venezuela) specimens	88.1 \pm 4.2 (82.0–94.0) ($n=10$)	70.7 \pm 3.9 (63.0–78.0) ($n=10$)	25.2 \pm 1.0 (23.5–26.0) ($n=7$)	15.3 \pm 0.6 (14.5–16.5) ($n=10$)	/
<i>A.I. olivaceiceps</i> (Central Andes, Colombia) live birds	90.9 \pm 3.3 (79.0–98.0) ($n=199$)	78.9 \pm 2.6 (73.0–84.1) ($n=146$)	26.6 \pm 0.9 (23.5–30.6) ($n=149$)	18.3 \pm 1.5 (14.0–21.5) ($n=147$)	37.4 \pm 3.4 (22.4–47.5) ($n=209$)
<i>A.I. olivaceiceps</i> (Central Andes, Colombia) specimens	90.8 \pm 2.7 (86.0–97.5) ($n=25$)	74.3 \pm 3.2 (69.0–80.0) ($n=25$)	25.7 \pm 0.8 (24.0–27.5) ($n=25$)	16.3 \pm 0.9 (14.0–18.1) ($n=23$)	32.5 \pm 3.4 (29.0–37.0) ($n=4$)
<i>A.I. palpebrosus</i> (S. Colombia and N. Ecuador) live birds	92.1 \pm 3.0 (79.8–98.0) ($n=59$)	81.6 \pm 3.3 (71.5–89.9) ($n=54$)	27.6 \pm 1.8 (24.3–30.4) ($n=55$)	15.2 \pm 1.2 (12.7–17.5) ($n=54$)	35.3 \pm 2.2 (30.6–40.0) ($n=57$)
<i>A.I. palpebrosus</i> (S. Colombia and N. Ecuador) specimens	89.0 \pm 3.8 (79.0–99.0) ($n=68$)	75.0 \pm 3.4 (67.0–84.3) ($n=67$)	25.4 \pm 1.1 (23.0–30.0) ($n=66$)	16.1 \pm 0.9 (13.0–18.0) ($n=67$)	33.0 \pm 2.2 (30.5–38.0) ($n=10$)
<i>A.I. caerulecens</i> (S. Ecuador and N. Peru) specimens	87.5 \pm 3.1 (85.0–95.0) ($n=13$)	70.3 \pm 3.5 (64.0–74.0) ($n=12$)	24.8 \pm 1.6 (22.0–27.5) ($n=12$)	16.1 \pm 0.9 (14.5–17.2) ($n=12$)	/
<i>A.I. intensus</i> (West Andes, Colombia) specimens	91.7 \pm 4.0 (82.0–100.0) ($n=36$)	74.1 \pm 3.7 (67.0–81.3) ($n=36$)	25.5 \pm 1.3 (22.2–27.6) ($n=35$)	16.3 \pm 0.8 (15.1–18.1) ($n=34$)	37.0 ($n=1$)
<i>A.I. lacrymosus</i> (Peru) specimens	85.6 \pm 3.7 (77.0–92.0) ($n=13$)	69.5 \pm 2.8 (64.5–76.0) ($n=13$)	24.8 \pm 1.0 (23.5–26.5) ($n=13$)	15.5 \pm 0.6 (14.5–16.5) ($n=13$)	/